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THE LIFE-HISTORIES OF *MEGASTIGMUS SPERMOTROPHUS* WACHTL (HYMENOPTERA: CHALCIDOIDEA) AND ITS PRINCIPAL PARASITE, WITH DESCRIPTIONS OF THE DEVELOPMENTAL STAGES.*

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With one Text-figure.

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Introduction.

Following an intensive study on the genus *Megastigmus* Dalman carried out over the past three years, a more detailed knowledge of the life-history of *M. spermotrophus* Wachtl can now be presented.

Hitherto the only accounts available have been those of MacDougall (1906) and Miller (1916), which deal only with the broad outlines of the subject and give no details of the developmental stages. The latter are of special interest as the genus contains a gradation of forms ranging from the truly phytophagous to the parasitic in habit.

M. spermotrophus is restricted in its host range to the Douglas Fir, *Pseudotsuga* Carr. and earlier records of its emergence from seeds of Silver Fir (*Abies spp.*) probably refer to *M. rafni* Hoffmeyer (Hussey, 1952).

* Based on part of a thesis submitted for the degree of PhD. of the University of Edinburgh.

II. *Megastigmus spermotrophus* Wachtl.

(1) *The Developmental Stages.*

Egg. The egg of *M. spermotrophus* is composed of three distinct regions: (1) a long anterior pedicel, (2) an elongate-oval body and (3) a short spur-like posterior pedicel. The average lengths of these portions are: anterior pedicel 0·90 mm.; body length 0·30 mm., width 0·135 mm.; and posterior pedicel 0·130 mm. Soon after deposition the anterior pedicel collapses and becomes a ribbon-like filament attached to the body of the egg.

First Instar.—This instar possesses a head and 13 body segments. It is minute, invisible to the naked eye, translucent in colour with a tendency to pale yellowish-green in older individuals. The shape is somewhat fusiform, being broader anteriorly and tapering towards the posterior extremity. The head capsule, only slightly narrower than the first thoracic segment, is hemispherical with a pair of blunt tubercles representing the antennae which are only visible under high magnifications. Each body segment bears on its anterior border two bands of very minute spines with occasional interspersed papillae forming a third row. All segments are devoid of setae and there is no evidence of a respiratory system.

Specimens of this instar range from 0·23–0·48 mm. in length. The extremely sharp, pale golden and slightly curved mandibles overlap at the tips and measure from 0·012–0·017 mm.

Unlike the primary larvae of many other Chalcids, *Megastigmus* lacks sensillae on the labrum. The sensillae representative of the maxillary and labial palpi are present, as are a further pair within the hypostoma common to most other Chalcids.

Second Instar.—The individuals of this stage are very similar to the first instar, but the shape is less fusiform and, as the thoracic segments have increased in width, the head appears proportionately smaller. The individual body segments are more conspicuous and translucent, greyish-white except in the region of the alimentary canal which is pale yellowish-green. Setae and anterior bands of spines are absent. In glycerine mounts the respiratory system shows as two lateral longitudinal trunks.

The mandibles are now quadridentate and triangular in shape, with very sharp teeth. The tip is golden but the rest colourless. The size ranges from 0·025–0·041 mm.

Specimens of this instar measure from 0·30–0·60 mm.

Third Instar.—Larvae of this stage are less attenuated posteriorly and are more arched. They are greyish-white, but the large alimentary canal remains yellowish-green. The respiratory system is more advanced, with the longitudinal tracheal trunks united anteriorly but not posteriorly. There are no setae or spiracles present.

The mandibles are quadridentate and more heavily chitinised, with teeth more closely set than in previous instar. The size ranges from 0·047–0·060 mm.

Specimens referable to this instar have a body length from 0·5–1·5 mm.

Fourth Instar.—This instar closely resembles the previous stage and is only safely separable by mandibular measurement. The body is strongly arched and cylindrical, with little evidence of taper. The alimentary tract is larger and its contents tend to give the larva a pale green colour. The respiratory

system is well developed with the longitudinal tracheal trunks united posteriorly as well as anteriorly. Numerous lateral branches pass out to the internal organs. In older larvae of this instar the developing spiracular trunks can be seen. A depression at the hind end of the body marks the anus. The sensillae of the labial region are now visible, but setae are still absent. The pale amber triangular mandibles measure from 0·70–0·85 mm.

Body length of this instar ranges from 1·00–2·4 mm.

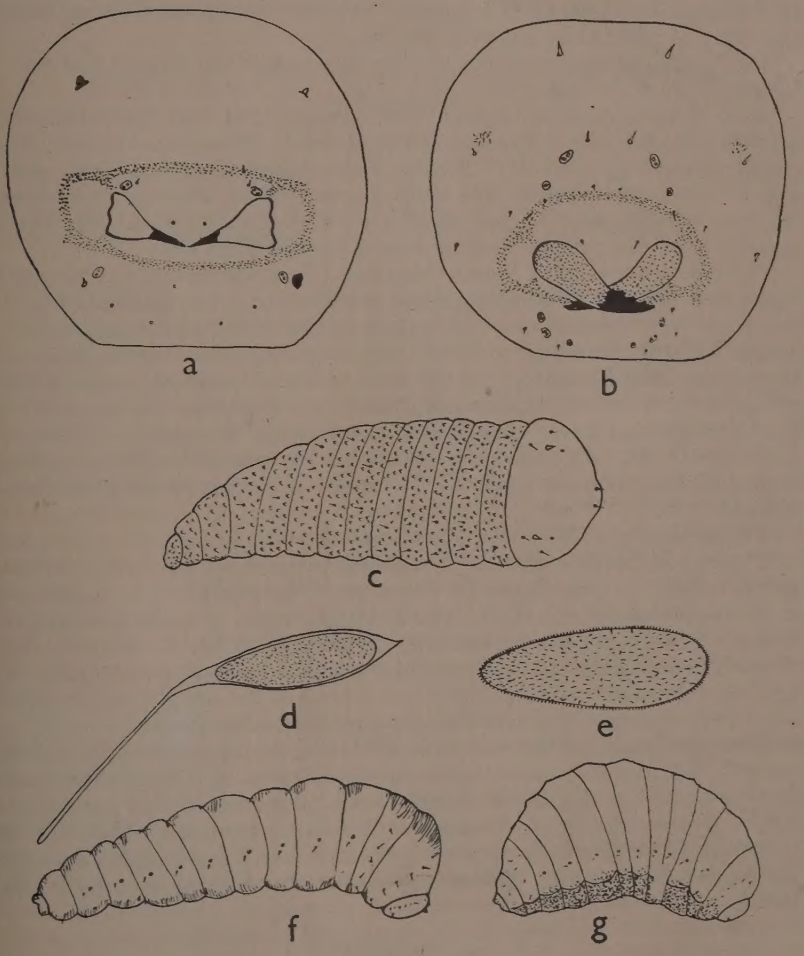

FIG. 1.—*a–b*, Head capsule of larva of (*a*) *Amblymerus apicalis* Thomson. (*b*) *Megastigmus spermotrophus* Wachtl. (*c*), First instar larva of *A. apicalis*. (*d–e*), Egg of (*d*) *M. spermotrophus*. (*e*) *A. apicalis*. (*f–g*), Mature larva of (*f*) *A. apicalis*, (*g*) *M. spermotrophus*.

Fifth Instar.—Fifth, final instar, larvae are white to dark grey in colour according to the quantity of fat-body obscuring the grey contents of the alimentary canal. As they reach full growth the body becomes strongly arched with conspicuous intersegmental folds. The head is a rigid hemispherical capsule on which the antennae are represented by a pair of sensillae, each with two pits. The larger setae are fairly constant in position, but several smaller ones are variable in occurrence. The pairs above and between the antennae, outside and ventro-lateral to the antennae and a pair ventral to the mandibles are always present. Other sensillae universally present are those representing the antennae, labial and maxillary palpi. Occasionally the maxillary and labial setae may be replaced by placoidal sensillae.

The quadridentate mandibles are bluntly toothed and heavily chitinised. Length: 0·095–0·116 mm.

Each thoracic segment carries a circle of setae. The first carries six setae on each side, the second five and the third three. These setae become progressively smaller posteriorly. The first eight abdominal segments each carry a seta behind the spiracle. The ninth segment carries three pairs of setae, one pair dorso-lateral and two pairs latero-ventral in position. The tenth segment bears two pairs of setae above and one below the anus.

Spiracles are present on thoracic segments II and III, as well as abdominal segments I to VII. These spiracles are connected to the longitudinal trunks, and from these junctions tracheae and tracheoles ramify to the various body organs. All the spiracles are similar in shape and size, but those on the thoracic segments are slightly larger. The spiracle consists of a large ellipsoidal atrium with a circular aperture below which the trachea diminishes in size gradually until it reaches the valve. The latter is recognised by its transverse and longitudinal striations. An unusual feature is a minute tube leading from the inner surface of the atrium posteriorly to the surface of the first intersegmental fold behind.

Size range of the fifth instar is from 1·8–4·0 mm.

Pupae.—Initiation of the prepupal phase is marked by the passing of faecal pellets for the first time during development. The body of the larva becomes more strongly arched and rapid internal changes begin. The abdominal region becomes increasingly smooth and appears reflexed at the caudal end. The thoracic region develops the conspicuous imaginal wing-buds and within the prothorax the adult head becomes visible by reason of the orange-pink compound eyes. The average duration of this prepupal phase is three days.

A complete and detailed account of a *Megastigmus* pupa is given by Milliron (1949) for *M. nigrovariegatus* Ashmead which agrees with that observed in *M. spermotrophus*. Pigmentation commences in the latter after about seven days. By the eighth day hairs appear on the wings, thorax and abdomen. On the eleventh day the body begins to assume a yellow-brown coloration with the wings almost black. The males mature two or three days before the females.

II. Life History.

There are in the literature many comments upon the extended period of emergence of the adults. Hoffmeyer (1930) and Wolf and Jenss (1941) speak of various peaks of emergence during the spring and summer. These observa-

tions must refer to seed kept in the laboratory, for in the field there is a relatively restricted emergence period. During the present study seed kept in the laboratory yielded *Megastigmus* adults from February to August, but in the forest the emergence was complete in fourteen days even in areas as far apart as Kent and Ross-shire. The commencement of emergence naturally depends on the temperature and, following laboratory rearings at different constant temperatures, the threshold of development of the pupal phase was calculated as 42·5° F. Using this developmental zero and observing the time required to complete the pupal phase, it can be shown that the amount of heat required to complete pupal development is about 390 day-degrees.

TABLE I.—*Effect of temperature on the duration of the pupal phase in* Megastigmus.

Temperature °F.	77°.	66°.	57°.	49°.
Length of pupal phase in days .	11·0	16·0	28·0	60·0
Developmental zero °F. . . .	42·5	42·5	42·5	42·5
Effective temperature . . .	34·5	23·5	14·5	6·5
Day-degrees of heat required . .	379·5	376·0	406·0	390·0

Observations made in the forest at Bedgebury, Kent, where a standard meteorological station was situated alongside the trees under study, showed that the adults were on the wing within two days of the date calculated. This date for emergence was determined by using the sum of the *effective* temperatures, i.e. the excess of the daily mean temperature above the developmental zero of 42·5° F. In general the adults are flying sometime between mid-May and mid-June. The males emerge from two to four days before the females.

In the laboratory at 59° F. the average longevity of males was 6·9 days and females 9·5 days. At higher temperatures these periods decreased to as low as less than one day at 90·0° F. Cooler conditions (43° F.) increased the duration of life to 14·9 days for males and 19·4 days for females. Wolf and Jenss (1941) postulated that in the forest females would live for about a month. As the emergence lasts about a fortnight the longevity of the latest females to emerge determines the period of activity. At Bedgebury the total period of adult activity lasted about a month, so that the females probably live about three weeks.

Emergence is effected by cutting a small circular hole in the testa of the seed. Evidence was obtained to show that the range in size of individual *Megastigmus* was correlated with the size of the seeds.

Once on the wing the adults tend to hover around the apices of the newly flushing shoots of the host tree, where copulation takes place on the needles. The male approaches the female and examines her with vibrating antennae; after a few seconds his antennae are held rigid at 45°, whilst those of the female continue to vibrate. Keeping his feet stationary, he oscillates his body from side to side until the female moves to within about half a centimetre, when he mounts her back. He stands with his fore-legs on her head, middle legs on her thorax and hind legs on her folded wings. During the initial courtship the antennae of the male vibrate very rapidly through a small arc in close proximity to those of the female. Occasionally he moves them through a wider arc and

brings them into contact with the basal joints of the antennae of the female. Each of these larger sweeps of the antennae is accompanied by a distinct lurch forward of the body, which brings the heads of the copulating pair into contact. When the female is ready to copulate she slowly lowers the sterna in order to expose the genital opening. The male instantly slips off backwards and copulates caudo-laterally. Courtship normally lasts for one or two minutes and coition for fifteen to twenty seconds.

Olfactometer tests with unfertilised females showed that, before fertilisation, females were not attracted by the odour of the host tree. This presumably accounts for the fact that in mixed woods adults have been observed hovering around the branches of several different species. Once fertilised, however, the female is attracted to the odour emitted by fresh needles of Douglas Fir. Such an olfactory response reduces the area within which the female must search for cones. These tests were made with a simple olfactometer of the type suggested by Grosch (1950).

Having located a cone, the female examines the surface with her antennae (Miller, 1916) until a suitable seed is found. She then stands on an ovuliferous scale, always facing the base of the cone, and inserts her ovipositor into the apical third of the exposed portion. The abdomen is elevated and the caudal end arched forward, thus permitting the ovipositor to assume a perpendicular position at the mid point between the widely spread middle and hind tarsi. Dorso-ventral body movements commence accompanied by a flexing of the legs, which produce a series of alternate thrusts and withdrawals, so driving the ovipositor down. After some 30–60 seconds the ovipositor sheaths are withdrawn while the ovipositor is forced down until the whole body lies against the cone-scale. The tip of the ovipositor passes through the ovuliferous scale on which the female stands, together with its underlying bract, and reaches down to the second or third scale below the surface of the cone. It passes to the centre of this scale, almost at its base, and then turns forward into the seed on its upper surface. After depositing the egg within the endosperm of the seed the ovipositor is withdrawn rapidly. The whole operation lasts from two to five minutes.

Observation in the field suggests that the incubation period of the eggs is relatively short and does not exceed five days. Although, on occasion, more than one egg may be laid in a single seed—as many as seven eggs in one seed embryo were found—only one can successfully complete its development. It is possible that in such cases all the larvae in the seed would die of starvation but, despite hundreds of dissections, this was not observed. To test this in the field a group of cones growing in close proximity on the same branch were chosen, on the assumption that they would probably have received the same attention from the *Megastigmus* females. Twelve of these cones were removed from the tree in late June, whilst the rest were covered with muslin to prevent the possibility of further oviposition, and allowed to grow on until the autumn. The sleeved cones were subsequently found to contain 219 fertile seeds of which 208 were infected with *Megastigmus* and contained mature larvae. The twelve cones removed in the late spring proved to be infected with eggs at the rate of 95 per cent. of the sound seed. Of this proportion infected 17 per cent. contained more than one egg per seed. If 95 per cent. of the seed within those cones sleeved until the autumn was infected we should expect to find about 208

larvae in the 219 fertile seeds. As reported above, this was so, indicating that even in those cases where more than one egg was deposited in a seed only one larva completed its development.

Oviposition normally occurs over a period of about three weeks, but the effective length of this period may be affected considerably by the differing phenologies of tree and insect.

Examination of the female ovaries suggests that each female is capable of laying at least fifty eggs within a few days of emergence, as each of the fourteen ovarioles contains at least two or three ripe eggs. Data will be presented elsewhere to show that under conditions of low *Megastigmus* density as many as 150 eggs may be laid by each female.

By sleeving unfertilised females upon cones it was shown that *M. spermotrophus* is capable of facultative parthenogenesis. Eight virgin females produced eighty offspring, all males. This ability of the females to produce viable male-producing eggs, even though unfertilised, has a profound effect upon the sex-ratio. This phenomenon accounts for the wide range of values given to the sex-ratio in the literature. Taking all the rearings together over a period of three years the ratio is almost 1:1 as 11,248 males and 11,342 females emerged. Flanders (1939) suggested that arrhenotokous Hymenoptera determine the sex of their eggs at the time of oviposition, the discharge of sperms from the spermotheca being prevented when oviposition is attempted in " unpreferred " hosts under conditions of low host density and high parasite density. Figures obtained in Ross-shire showed that where the density of *Megastigmus* per cone was very high—16 adults per cone—the adults emerging the following year were predominately males. At all lower densities there were slightly more females than males.

No records of the feeding-habits of the adults are given in the literature although Milliron (1949) mentions that he kept specimens alive on cotton-wool soaked in sugar solution. This technique was successfully used in the present study. In the field intensive searching of flower-heads in the vicinity of infected host trees failed to reveal adults taking nectar, but Mr. C. N. Hawkins informs me that he swept a number of females from flowers at Minehead in June, 1952. Feeding was, however, observed on the excretions produced by the sistentes generations of *Adelges cooleyi* on Douglas Fir. This observation has proved most interesting in the light of the discovery by Ermin (1950) that the " honeydew " produced by *Cinara pichtae* is used as a source of protein by bees in Turkey. It is conceivable that *Megastigmus*, like many other Chalcids, needs to assimilate protein before it can lay viable eggs and, although phytophagous, has developed this association with *Adelges* to make up the deficiency.

The eggs are laid within the seed at random, but within a day or so of hatching the young larvae migrate to the region of the archegonia. As the seed develops the endosperm becomes firmer in consistency and is white in colour with the pale green cotyledons appearing along the central axis. At this time the *Megastigmus* larva is usually located at the distal end of the seed, where it commences to feed on the embryonic cotyledons. The basal portion of the seed and the outer periphery of the endosperm remain intact until after the larva has reached the fourth instar. Following this the entire contents of the seed are consumed apart from a white papery envelope immediately below the testa, which remains intact. This white lining to the seed is invaluable in

detecting infected seed which, after being shed from the cone, is attacked by rodents.

Larval development is very rapid. All the instars are passed through within six to seven weeks during the late spring and early summer. The duration of the successive instars was recorded as: Instar I, 3–5 days; Instar II, 5–10 days; Instar III, 5–10 days; Instar IV, 7–10 days and Instar V, 10 or 22 months.

III. Flowering Biology of Douglas Fir.

The cone of Douglas Fir is only suitable for oviposition during a fairly well-marked period of growth, which has not hitherto been defined.

Two forms of Douglas Fir occur in Great Britain, but only the Oregon or Green form, *Pseudotsuga douglasii* Carriere, is widely planted, as the Blue or Colorado form, *P. glauca* Mayr, is subject to heavy defoliation by the fungal leaf-cast disease Rhabdocline. The cones of these species are easily distinguished by the following characters:

P. douglasii.	*P. glauca.*
Cones green.	Cones pink.
Bracts not reflexed.	Bracts always strongly reflexed.

Following field observations it is possible to define the stage of growth of the cone during which it is susceptible to attack by *Megastigmus*. In the case of *P. douglasii* the cones are from one and a half to three inches in length, with the exposed portion of the bracts three-quarters of an inch long and held tightly against the surface of the cone. The ovuliferous scales are very pale green in colour with a reddy-brown coloration appearing towards the base of each scale, where it is overlapped by the scale below. By the time this brownish suffusion has spread to all but the apical fringe of the scales the cone tissues begin to get tough so that ovipositing females become trapped by their ovipositors.

In the case of *P. glauca* the susceptible period occurs when the cones are from one and a half to two and a half inches long, with the exposed portion of the reflexed bracts about half an inch long. The ovuliferous scales are deep mauve-pink except where overlapped by the scale below, when a narrow fringe of pale green appears. The bracts are pale green with the mid-rib and lateral margins dark green.

Allen (1941, 1942 and 1943) has investigated the subject of seed production in the Douglas Fir and gives a summary of its flowering biology. The reproductive strobili are differentiated in August and by early March free microspores are produced which, by the end of the month, become ripe pollen. The reduction division of the megaspore mother-cell occurs early in March, but pollen remains in the micropyle of the seed for three weeks without germinating. Then, following five weeks' growth, the tip of the pollen tube reaches the nucellus and penetrates the archegonium a week later. Thus, on the average, fertilisation takes place about nine weeks after pollination. In Great Britain the " red-flowering " stage of the Douglas Fir appears in the last two or three weeks of April so that fertilisation is delayed until late June or early July.

As the flowering strobili are laid down in August of the year before coning the size of the cone crop will be largely governed by the weather immediately

preceding that time. Roeser (1941) has shown that the weather conditions during pollination markedly influence cone production, frost being especially inimical to the young flowers. We may, therefore, infer that, as the proportion of the seed attacked by *Megastigmus* is correlated with the size of the cone crop, the following factors will have an influence on the amount of damage : (1) The weather at the time of pollination, (2) the weather of the penultimate summer, (3) the weather prior to oviposition in as far as it influences the phenology of host and parasite and (4) the weather during oviposition affecting female fecundity.

It is not as yet possible to forecast the size of cone crops more than one year ahead, but in those coniferous species with an irregular periodicity of cone production there is good evidence (Lochwing, 1940) that drought, by retarding vegetative growth, increases the carbon/nitrogen ratio and hence tends to increase the amount of flowering the following year. Tirée (1935) has pointed out that abundant flowering reduces the number of vegetative buds so that the reduced photosynthetic surface the following year reduces the possibility of two successive cone-years.

IV. Differential Effect of Weather on *Megastigmus* and its Host.

The host tree appears to mature its cones to the stage of growth at which it is susceptible to attack by *Megastigmus* with less dependence on temperature than is exhibited by the Chalcid, whose emergence is markedly influenced by the weather conditions. Wolf and Jenss (1941) noted that cold weather retarded the development of *Megastigmus* more than that of Douglas Fir flowers. The inference of the present study is that adult female *Megastigmus* are on the wing over a longer period than that during which the cones are suitable for oviposition. Hence in a " late year " a proportion of the cones will have developed too far for successful oviposition by the late emerging Chalcids. In an early year the wasp population will decline and die out before a proportion of the cones has reached a suitable stage for oviposition. In 1952, at the Bedgebury National Pinetum, the wasps had been on the wing for three weeks before the cones of some *P. douglasii* had reached a stage suitable for oviposition, and although surveys showed that the remaining *Megastigmus* were concentrated on these cones a high proportion of the seed escaped attack. The average number of eggs laid per seed in these late maturing cones was only 0·17, whilst in the earlier cones of *P. glauca* a level of almost 2·0 eggs per seed was found.

Table II illustrates how such a lack of synchronisation occurs. In the " early " year 1952 the earliest date of *Megastigmus* emergence was advanced as

Table II.—*Phenology of* Megastigmus *and its host.*

Mean Temperatures :	1951.	1952.	1953.
January	39·5	37·0	36·1
February	38·9	35·8	37·9
March	40·6	43·8	44·2
April	42·5	48·2	46·7
May	50·5	54·7	52·5
Date of first *Megastigmus*	June 4	May 21	May 20
Dates when most Douglas Fir cones appeared past the suitable stage	June 13	June 8	June 10

much as fourteen days, whilst the trees were on the average only about five days ahead of 1951.

V. Extended Diapause in *Megastigmus* Larvae.

From the standpoint of bionomics the extended diapause of certain fifth instar *Megastigmus* larvae is of some importance. Some larvae do not pupate until the spring of the third year after they have reached maturity. Experiments were conducted to measure the effect of temperature and humidity upon this property of extended diapause.

Seed collected in October was kept in a refrigerator at about 38° F. At intervals samples of 100 seeds each were placed at different constant temperatures above the developmental zero of 42·5° F. The emergences were recorded daily and, when emergence was complete, the sample dissected to determine the percentage remaining in diapause. These results are summarised in Table III which shows that, at all temperatures, a minimum exposure to cold was necessary before any emergence took place at all.

Table III.—*Effect of temperature and duration of cold-rest on diapause in* Megastigmus.

Duration of cold-rest in weeks	0	2	4	5	8	9	12	15	20	25	27	30	40
Mean duration of exposure of seed at 77° F. before emergence (in days)	—	—	—	40	30	28	26	21	13	15	38	62	106
Percentage larvae remaining in diapause	—	—	—	88	49	44	47	32	29	34	49	60	75
Duration of exposure at 66° F.	—	—	—	—	37	36	35	29	19	36	—	—	—
Percentage larvae remaining in diapause	—	—	—	—	58	58	52	39	36	42	—	—	—
Duration of exposure at 58° F.	—	—	—	—	—	—	59	50	38	55	—	—	—
Percentage larvae remaining in diapause	—	—	—	—	—	—	58	52	36	48	—	—	—

With increasing duration of exposure to cold the amount of heat required to complete development (as measured by the number of days exposure to high temperature to effect emergence of the average individual in each sample) decreases. Similarly, the proportion remaining in diapause decreases. However, after about 25–27 weeks' cold-rest both these values start to increase again. Such a lengthening of the developmental period suggests that a cyclical phenomenon is operating in the diapausing larvae, the response to higher temperatures rising gradually to a peak and then falling off again. It should be noticed that this peak was reached about the middle of April regardless of the temperature to which the samples were exposed after removal from cold-rest. The lengthening of the necessary period of exposure to higher temperatures before emergence could be due to (1) an increase in the period of time before initiation of the pupal phase or (2) to a lengthening of the pupal phase. This was put to the test by extracting larvae from seed after various periods of cold-rest and placing them in samples of 50 for observation in small Petri dishes. The larvae were examined every day and the date of excretion of the faeces—which marks the initiation of the pupal phase—noted.

TABLE IV.—*Effect of temperature on the pupal phase of* Megastigmus *females.*

Temperature.	77° F.				66° F.			58° F.	
Mean duration of pupal phase	11	11	11	11	16	16	16	26	26·2
Number of days before excretion	18	15	0	51	20	19	20	34	29
Period of cold-rest in weeks	9	12	23	30	9	12	23	12	23

These results show conclusively that, once initiated, the duration of the pupal phase is determined by the environmental temperature.

Hinton (1953), following a critical review of the current theories on diapause, draws the conclusion that the phenomenon is brought about by a conjunction in time of two quite distinct processes: (*a*) a diapause hormone must arrest growth in most tissues and (*b*) the prothoracic glands, which induce moulting and inhibit the action of the diapause hormone, must cease to secrete. Furthermore, it is clear that the secretion of the prothoracic glands is only the *immediate* cause of the termination of diapause and that the determinant of its duration is not these glands, whose secretory activity is governed by the brain. In *Megastigmus* whatever causes the brain cells to secrete again must have an annual rhythm superimposed on the necessity for cold-rest.

Table III also illustrates the point that, following a period of cold-rest, the proportion of the larval population remaining in diapause becomes greater the lower the " high " temperature to which it is subsequently exposed.

VI. The Effect of Humidity and Contact Water on Diapause.

Ullyett (1936) studied the function of the cocoon in maintaining the microclimate of *Microplectron fuscipennis* and Prebble (1941) adopted his methods in experiments on the role of the cocoon in regulating the water exchanges of *Gilpinia*. The reasoning employed by these investigators has been used as the basis of the following conclusions.

The larvae of *M. pinus* (which were used in this work to facilitate handling due to their larger size) were found to make up 15·8 per cent. of the gross weight of the seed of *Abies nobilis* in the autumn (Table V). Their water content, calculated by heating to dry-weight in an oven at 100° C. for three hours, was found to be 57·7 per cent. of their live-weight in November, which was 4·63 mg. The subsequent values assume that all the weight loss occurring was due to loss of water but, as Prebble found with *Gilpinia*, this is essentially correct, for the average oven-dry weight of the larvae only fell from 1·90 to 1·81 mg. over the six months of diapause.

TABLE V.—*Ratio larval wt./gross wt. in spring.*

	Gm.	Gm.	Gm.	Gm.
Weight of seed + larvae	1·1840	0·9930	1·1171	0·9747
Weight of empty seed coats	0·9981	0·8365	0·9880	0·8168
Weight of extracted larvae	0·1859	0·1565	0·1831	0·1579
Larval weight as percentage gross weight	15·7	15·7	15·6	16·2

To illustrate the efficiency of the microclimate in conserving water, whole seeds, empty seed-coats and naked larvae were exposed to a Saturation Deficiency of 13·0 mm. (Table VI). The water-loss from the whole seeds was greatest in the first two days, but after losing 6·9 per cent. of their original weight in nineteen days they lost weight imperceptibly. Subsequent studies on the water contents of the seed coats and contained larvae of these " whole " seeds showed that the water content of the testas fell from 12·7 per cent. to 8·9 per cent., whilst that of the larvae fell from 57·7 per cent. to 51·9 per cent. Naked larvae, similarly exposed, experienced a loss of 14·4 per cent. of their original weight, their final water-content being 52·0 per cent. Empty seed-coats lost 7·6 per cent. of their weight, the water-content being reduced from 12·7 per cent. to 5·7 per cent. Part of the water-loss of the whole seeds related to moisture in the testa and part to the contained larva. The exact proportion can be calculated as follows : The seed coat constitutes 84·2 per cent. of the combined weight of the seed and larva, but it is known from the data above that the percentage loss of the initial weight of the testas was 7·6 per cent. after thirty-four days' exposure to a S.D. of 13·0 mm. Under the same conditions the loss of initial gross weight of seed and larvae = 6·9 per cent.

Therefore loss from seed coats $= 7{\cdot}6 \times 0{\cdot}842$.
$= 6{\cdot}4$ *per cent. of initial gross weight.*

Hence, balance of gross weight loss attributable to contained larvae $= 6{\cdot}9 - 6{\cdot}4$
$= 0{\cdot}5$ *per cent of initial gross weight.*

This loss in terms of initial larval weight $= 0{\cdot}5$
$= 3{\cdot}2$ per cent.

Under the same conditions, naked larvae lost 14·4 per cent. of their initial total weight, which demonstrates the efficiency of the microclimate in conserving water.

TABLE VI.—*Weight losses of seed and larvae exposed to Saturation Deficiency of* 13·0 *mm.*

Period of Exposure.	Percentage loss of original weight. Naked larvae.	Empty testas.	Whole seed.
2 days	3·3	6·6	4·5
4 ,,	5·9	6·9	5·3
7 ,,	7·9	7·2	5·8
12 ,,	9·9	7·4	6·2
19 ,,	13·3	7·6	6·8
27 ,,	14·4	7·6	6·8
34 ,,	14·4	7·6	6·9

To investigate the effect of exposure to contact water or a saturated atmosphere on the larvae within seed it is necessary to calculate a value for the initial larval weights. This may be done by two methods :

(*a*) Average initial gross weight of seed = ·04203 gm.
,, ,, larval weight = ·04203 × ·158
= ·00664 gm.

(*b*) Average gross weight (seed + larvae) after exposure to 100 per cent. relative humidity for 45 days = ·04845 gm.
Ratio $\frac{\text{larval weight}}{\text{gross weight}}$ after exposure = 11·3 per cent.
Original larval weight prior to exposure of seed = ·04845 × ·113
= ·00547 gm.

The average of these estimates, 0·00605 gm., is the best approximation of the true larval weight at the beginning of the experiment. The final weight of the larvae, found by direct weighing following extraction from the seed, was 0·00463 gm., indicating that they were losing water despite the saturated environment outside the seed. It is thus apparent that the microclimate within the seed is kept near saturation, otherwise the loss of water from the larva could not take place. Maintenance of this microclimate is, however, achieved at the expense of the insect, since, in dry air, the testa merely delays the continuous loss of water from the larval tissues. Reference to Table VI shows that the loss of water, even in dry conditions, becomes progressively less with increasing duration of exposure. Thus, when the water-content of the larvae has fallen to 15·3 per cent., further loss is restricted by some physiological adaptation, which probably accounts for the fact that larvae extracted from the seed will pupate successfully after as long as six months' exposure in an open Petri dish.

In view of the important function of the seed-coat in reducing water-loss and the findings of Prebble that saw-fly cocoons were inhibited from development in unsaturated environments, a number of *Megastigmus* larvae were exposed to different humidities (Table VII). These humidities were controlled by salt solutions, as used by Shulov (1952).

TABLE VII.—*Effect of relative humidity on termination of diapause in* Megastigmus.

Relative humidity.	Number of larvae.	Number dead.	Percentage mortality.	Percentage prolonged diapause.	Days to adult.
100	50	18	36·0	54·0	29
90–91	50	13	26·0	54·5	31
83–85	50	4	8·0	52·0	32
71–74	50	3	6·0	54·0	34
50–53	50	1	2·0	55·5	39
29–31	50	0	0	54·0	45
18	50	0	0	52·0	54
0	50	0	0	50·0	62

These results show that the percentage of larvae remaining in diapause varies within sufficiently narrow limits to suggest that the humidity of the environment has little effect on the initiation of pupation. Mortality of the larvae is obviously correlated with the humidity, probably due to the physical require-

ments of the disease organisms. The lengthening of the period of development with decrease of humidity suggests that shortage of water delays the complex physiological processes associated with pupation.

Table VIII includes results in which the effect of contact water was compared with saturated air and laboratory conditions. Again, however, the proportion was not significantly affected, although development took slightly longer in the drier conditions.

TABLE VIII.—*Effect of "contact" water on termination of diapause in* Megastigmus.

Treatment.	Number of larvae.	Second diapause. Number.	Second diapause. Per cent.	Number of days to maturation.
Seeds in dry tube . . .	90	47	53·2	15·1
Seeds at 100 per cent. R.H. .	93	49	52·2	11·1
Seeds kept in contact with water	89	48	53·8	11·0

Advantage was taken of the considerable collections of Douglas Fir seed made by the Forestry Commission in 1951 to calculate the mean percentage of larvae in prolonged diapause in that year in different areas. These results showed a surprising uniformity for England and Wales at about 16 per cent. The present study yielded figures of the order of 55 per cent. for the North of Scotland.

The experiments above have provided evidence that, however favourable the conditions, a small proportion, about 10 per cent., have the tendency to diapause for the extra year genetically fixed. The figures obtained in the field suggest that the lower spring temperatures in the North may cause an additional percentage larger than further South, to remain in diapause.

VII. *Amblymerus* ? *apicalis* Thomson, the Principal Parasite of *Megastigmus*.

Three species of parasites have been reared in the laboratory on larvae of *Megastigmus* and these were kindly identified by Mr. G. J. Kerrich of the Commonwealth Institute of Entomology, and Mr. M. W. R. de V. Graham of the Hope Department of Entomology, Oxford, as *Trichomalus* sp. near *sunides* Walker, *Anogmus strobilorum* Thomson and *Amblymerus ? apicalis* Thomson. Only the last, however, is sufficiently common to be of economic importance. All three are Pteromalids, but may be differentiated by the following key :

Females

1 (2) Ovipositor strongly exserted, insect blue-green in colour **Anogmus strobilorum**

2 (1) Ovipositor not strongly exserted, insect coppery-green.

3 (4) More than 2·5 mm. long. Propodeum lacking bulbous enlargement . . . . . **Amblymerus apicalis**

4 (3) Less than 2·5 mm. long. Propodeum with a conspicuous bulbous enlargement posteriorly . . . . . **Trichomalus sp.**

Males

1 (2) Coppery-green with an orange band around abdomen **Amblymerus apicalis**

2 (1) Not so coloured.

3 (4) Blue-green in colour . . . . . **Anogmus strobilorum**

4 (3) Propodeum with a " boss " as in female, iridescent coppery-green **Trichomalus spp**

(1) *Taxonomic Description.*

Female.—Head slightly broader than thorax, three times as broad as long at the middle, occiput distinctly concave ; post-ocellar line equal to twice the ocellocular line, which is itself three times the diameter of an ocellus. Viewed from in front the head is broader than high (1 : 0·75), narrowed below the eyes, truncate at the mouth ; malar space equal to not more than 0·375 of the eye height ; antennal scrobe shallow ; eyes moderately large, ovate, bare ; clypeus finely striated, rest of head nearly uniformly finely reticulate-punctate ; right mandible distinctly quadridentate, left mandible tridentate ; inner tooth broad and very slightly concave at the apex ; maxillary palpi 4-segmented. Antennae 13-segmented, inserted a little below middle of head (1·25 : 1) on a line with the lower extremities of the eyes, distinctly clavate ; scape attaining the level of the top of the compound eyes, subcylindrical ; pedicel a little more than twice as long as broad at the apex, not quite as long as the ring segments plus the first funicle segment ; three distinct ring segments, the first smallest ; funicle 5-segmented, the segments successively increasing a little in width and decreasing very slightly in length ; first funicle segment a little longer than broad, about equal to the three ring segments combined ; fifth segment of funicle a little broader than long ; club distinctly thicker than funicle, ovate, a little longer than the two preceding funicle segments ; funicle and club segments clothed with short inconspicuous hairs.

Thorax slightly more than one and a half times as long as broad ; pronotum short, the dorsal aspect transverse, a little narrower than the mesonotum, and nearly in the same horizontal plane as the mesoscutum, sculptured like mesoscutum, the anterior declivity nearly perpendicular ; mesoscutum slightly convex, finely reticulate-punctate at the sides, but more coarsely punctate dorsally, about one and a half times as long as broad (1 : 1·52) ; the parapsidal grooves weakly impressed anteriorly but effaced posteriorly ; scutellum sculptured like mesoscutum, especially posteriorly and anteriorly, elsewhere a tendency to be finer, convex, distinctly shorter than mesoscutum, slightly longer than broad ; axillae sculptured like lateral portions of scutellum and broadly separated ; propodeum half as long as scutellum, without a neck, median carina present, lateral folds well developed and complete ; spiracular sulci shallow ; surface of propodeum between the folds distinctly wrinkled, laterally from folds finely reticulate ; spiracles circular ; pleura sculptured like dorsum, but upper portions of meso- and metapleura very finely reticulate.

Legs normal, hind coxae more markedly reticulate than others.

Fore wings about two and a half times as long as broad (1 : 2·4) extending beyond apex of abdomen, bare basally ; marginal cilia short ; marginal vein a little longer than postmarginal (1 : 1·1) and twice as long as stigmal vein (1 : 2·0). *Abdomen* ovate or conicovate, about as long as thorax and as broad or a little broader than thorax, smooth and polished dorsally at base, the apical tergites, all tergites laterally and the sternites with a faint reticulation. Tip of ovipositor barely visible from above.

Coloration.—Head, thorax and abdomen a shining, metallic coppery-green, antennal scape yellowish, rest of antenna yellowish below with dark brown marks dorsally, mandibles yellow-brown and brown at apices, rest of mouth-parts pale yellow. Coxae concolorous with thorax, rest of leg yellow-testaceous except apical tarsal segment which is brown. Wings hyaline, venation testaceous. Compound eyes with a black rim.

Length 2·5–3·7 mm.

Male.—Description of proportions and sculpture of parts as for female excepting the proportions between the veins of the wings which are : marginal : post marginal (1 : 1·05) and marginal : stigmal (1 : 1·31) and the fact that the antennae have two ring segments and six funicle segments.

Coloration of head and thorax as for female except antennae, which are entirely yellow apart from the black club and dorsal surface of pedicel. *Legs* as in female.

Abdomen coppery-green, devoid of reticulation on the shining basal area of the second segment. Its most conspicuous feature is the bright yellow band encircling the body at the apex of the second abdominal segment and the whole of the third and fourth segments. This yellow ring is interrupted at the base of the fourth abdominal segment by brown marks on each side.

Length 2·5–3·0 mm.

(2) *Life History and Habits.*

The adult *Amblymerus apicalis* cuts its way out of the seed by means of a neat round hole, after the manner of its host. This emergence occurs towards the end of September and the insects remain on the wing for a considerable period. Even in the laboratory the average longevity of males was 49·4 days and that of females 65·9 days. To oviposit on their hosts the parasite must gain access to the seed, which means that eggs cannot be laid until the scales have opened far enough to allow the females to crawl beneath. By exposing seed and cones on the forest floor it was demonstrated that the parasite will not seek out its host once the cones or seed have been shed from the tree. It is thus feasible that in a season with favourable conditions, strong winds and low humidities, the seed may fall so rapidly as to prevent the female parasites attacking as many *Megastigmus* larvae as normal. This possibility is even more likely when the food requirements of the female before oviposition are considered.

Before oviposition the adults feed extensively on carbohydrates as provided by plant nectar, but before the female can produce visible eggs she must imbibe some of the body fluids of the host. She obtains these fluids by constructing a " feeding-tube " extending from the surface of the testa to the *Megastigmus* larva. Fluids rise up this tube by capillarity and are licked up by means of the ligula. The tube is constructed by puncturing the testa and host with the ovipositor, which is then withdrawn until only the tip penetrates the seed-coat. A viscid liquid exudes from it, which is twisted and drawn out downwards by the ovipositor until the body of the host larva is reached. The fluid hardens into a red-brown crystalline material, which appears on the outer surface of the testa in the form of a raised rim. The whole operation was observed to last about ten minutes.

Studies on the oocyte formation in *Amblymerus* showed that newly hatched females had no differentiation of the ovariole contents, and, until they were five to six days old the ovarioles were full of dense protoplasm. Between the sixth and tenth days differentiation into oocytes and nurse-cells occurred, although those females fed only upon carbohydrates did not develop their eggs further. Those given *Megastigmus*-infested seed had at least one fully developed egg within the ovarioles by the 13th–16th day. The total fecundity of field collected females was about forty eggs.

The ripe eggs were laid on the surface of the *Megastigmus* larva but not attached in any way, so that they were easily dislodged when the seed was

opened. Under field conditions these eggs remained unhatched until the following spring, but if brought into the laboratory at a temperature above 60° F. they hatched within a day or so. The egg is elongate, ellipsoidal in shape, 0·47 mm. × 0·22 mm., and is covered with a coat of short hairs so that it appears pitted in surface view.

The first instar larva is whitish-translucent in colour with remarkably curved scimitar-like mandibles. Each body segment is markedly tuberculate and segments 1–10 possess circles of setae. The head is very large relative to the thirteen tapering body segments and bears noticeable antennae. The young larva is very active and crawls about over the host, often curling its attenuated abdomen up into the air. When feeding, all stages of the parasite bury their heads into the host tissues. As material accumulates in the gut the larva becomes light-green in colour especially in the medial portion of the abdomen. Successive instars are characterised by a marked enlargement of the terminal abdominal segments so that the general body shape becomes weevil-like with a relatively small head bearing the conspicuous antennae. The tracheal system with nine pairs of spiracles and longitudinal tracheal trunks become completely developed in the second instar. When mature the only hairs present are a ring around the pro- and mesothorax with a single seta below each spiracle. The anus has two hairs above and below its orifice and segments 10, 11 and 12 bear two lateral setae in addition to the spiracular setae. As with *Megastigmus*, the moulted skin of the previous instar is often found loosely attached to the larva and provides useful evidence in determining the instar by reference to mandibular measurement.

TABLE IX.

Instar.	Mandible length. (mm.)	Body length. (mm.)	Duration in in days.
I	0·019	0·6	2–4
II	0·030–0·034	1·0–1·5	4–6
III	0·039–0·042	1·7–2·2	5–10
IV	0·060–0·064	2·4–2·7	5–10
V	0·079–0·086	3·0–3·5	

Throughout its growth the parasite feeds ectoparasitically upon the *Megastigmus* larva and within five weeks reduces it to a minute fragment of cuticle. When full-grown it closely resembles its host but even in the field the antennae are visible with a small lens. The field data obtained gave figures which suggest that the proportion of *Amblymerus* which enter diapause in any year is approximately the same as that of its host.

The pupa is of the normal hymenopterous exarate type. The head is directed ventrally with the tips of the mandibles apposed to the front coxae ; the antenna reach the front tibiae. The front leg appears alongside the pronotum, the middle leg is adjacent to the thorax between the front femur and the wing-pad. The proximal portion of the hind femur is concealed but the remainder of the hind-leg is visible, its tibia extend to the abdominal venter. The front wing-pad extends caudo-laterally, completely concealing the hind pads and parts of the legs indicated above.

Newly formed pupae are entirely white, but within a few days the compound eyes become distinctly pink and are deep crimson within ten days. The average pupal period of the male was 13·3 days, that of the female 18·5 days.

The sex ratio was 1·0 females to 1·6 males.

VIII. Summary.

1. The complete life cycle of *Megastigmus spermotrophus* Wachtl is presented with details of copulation and oviposition behaviour.

2. The larval instars are described.

3. The phenology of the Chalcid and its host are discussed and the effect of weather conditions upon damage to the seed of Douglas Fir described.

4. The stage of growth of the cones of Douglas Fir at the time of attack by *Megastigmus* is described.

5. Results of experiments on the extended diapause of the larvae are recorded. A minimum exposure to cold-rest was necessary for development. With increasing duration of exposure to cold-rest the amount of heat required to complete development decreased. Once initiated the length of the pupal period depended only on the temperature. Evidence of a cyclical phenomenon in the diapause is presented, the reponse to higher temperatures, following cold-rest, reaching a maximum and then declining.

6. Contact water and a saturated atmosphere are shown to have no effect upon the breaking of diapause, although the efficiency of the microclimate in conserving water is demonstrated.

7. A key to the Pteromalid parasites of *Megastigmus* is given.

8. The life-history and larval stages of *Amblymerus* ? *apicalis* are described.

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